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The morphology of Thallocarpus Curtisii

F. McAllister

(WITH PLATE 4)

The first published description of *Thallocarpus Curtisii* (Aust.) Lindb. seems to have been by Austin in 1869 (1). The simple structure of its sporogonium, which is without foot or elaters, naturally pointed toward a relationship to *Riccia*. In the dried material from which his descriptions were made the thallus appeared very like that of *Sphaerocarpos*. This, together with the fact of the spores adhering in fours, led him to believe that it must also be related to *Sphaerocarpos*. He believed it to be a genus intermediate between *Riccia* and *Sphaerocarpos* and gave it the name *Cryptocarpus*, the only species being *C. Curtisii*. The following is his description of genus and species:

"CRYPTOCARPUS (gen. nov.) Aust. MSS., 1864.

"Frons laxe spongioso-reticulata, irregulariter subpalmatim lobata, tenuis, epidermide hand distincta. Costa nulla. Radices intus non papillosi (ut in *Sphaerocarpo*), longissimi, intertexti. Fructus in frondis substantia immersus (ut in *Riccia*). Sporangia depresso-globosa, singulatim nata, non libera. Calyptra stylo nigro persistente coronata. Sporae 4-jugae (ut in *Sphaerocarpo*), vix solutae, in aspectu singulae et profunde quadrilobae."

"CRYPTOCARPUS CURTISII Aust. MSS. 1864.

"*Riccia Curtisii*, James, in Herb. (fide Curtis).

"Fronde caespitosa valde imbricata fibroso-papulata, laciniis inciso-lobulatis margine crenatis; sporangiis maximis in statu siccati latentibus sed frondes hume-

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actae sunt in substantia earum ut maculis nigris apparentibus; sporis fusco-nigris valde muricatis.

"On moist ground, South Carolina, Ravenel (In Herb. Sulliv., 1849). North Carolina, Curtis (l. c., 1853). 'Montand après Marseille' (Herb. Lanning, 'ex Herb. Torrey')."

Somewhat later (**10**) Lindberg called attention to the fact that the generic name *Cryptocarpus* was already in use, being used as the name of a genus of the Chenopodiaceae as well as for a genus in the Orthotrichiaceae. He proposed the name *Thallocarpus*, which is still in use. He makes no mention of having examined any plants and apparently on the authority of Austin's description places the genus in the Jungermanniaceae, class Cleistocarpae.

In 1877 Trevisan (**14**) proposed the name *Angiocarpus* as a substitute for *Cryptocarpus*. He placed the genus in the order Ricciaceae, tribe Riccieae, with *Ricciella*, *Riccia* and *Ricciocarpus*.

Austin in 1875 (**2**) referring to Lindberg's change of the generic name to *Thallocarpus** states that "the plant evidently belongs, with *Sphaerocarpus* (its nearest ally), to the Jungermaniaceae."

Later he refers again to *Thallocarpus* (**3**) having in the meantime studied fresh living material collected for him by Capt. John Donnell Smith in Florida. From this material he notes the striking similarity to *Riccia* "in which genus" he says "it should probably be included as a subgenus." He states that the adhesion of the spores of the tetrad "appears to be the only character in which it is decidedly different from *Riccia*." It is from this material that he determines the dioecious character of the liverwort.

This seems to be the literature that Schiffner has had access to in his account of *Thallocarpus* in Die natürlichen Pflanzenfamilien (**11**, p. 50). It is therefore surprising to find that Austin's latest reference to the plant has been overlooked or ignored and this genus placed in the subclass Jungermanniales and family Sphaerocarpoideae; in a family, the sporophyte of which is characterized by the presence of a foot and of sterile, "stärkereiche Nährzellen."

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* Although Lindberg proposed the name *Thallocarpus* he does not seem to have suggested the combination *T. Curtisii.* Austin makes use of this combination in 1875 but does not cite Lindberg as authority.

Stephani (12), under the name *Riccia Curtisii*, has elaborated the description of *Thallocarpus* from material "welche Pastor Curtis in seinem Garten gesammelt hat." He asserts that the plants which he examined were monoecious. In other respects his description does not seem to diverge in any important detail from that of Austin. He, however, insists that material from Austin's herbarium in the possession of Pearson corresponds fully with his description.

Thallocarpus is of common occurrence in the vicinity of Austin, Texas, during late winter and spring, growing most abundantly in sandy soil along with Riccias, *Sphaerocarpos*, and other liverworts. The plant studied corresponds very closely with those described by Austin if we take into account the essential corrections made in his later references to the liverwort. There seems little doubt that it should be regarded as the same species.

Because of the disagreement of Austin and Stephani as to the sex of the thallus of *Thallocarpus* I have examined a large number of thalli with this point in mind. Although a large number of plants of both sexes and of all ages were carefully dissected under a binocular microscope I was unable to find both archegonia and antheridia on any of the plants examined. Realizing the difficulty of detecting and recognizing immature sex organs in dissected material I have carefully examined paraffin sections of about fifty thalli, most of which were female. Part of these plants were sectioned to obtain material for a study of the morphology of the thallus and sporophyte, but special care was taken in each case to mount and stain the entire thallus. No case of the monoecious condition has been found in this material. The evidence seems fairly conclusive that *Thallocarpus*, as it occurs in the vicinity of Austin, is strictly dioecious.

I have accumulated considerable evidence to show that the four spores of the spore ball of *Thallocarpus* give rise to two female plants and two male plants as has been shown to be the case in *Sphaerocarpos texanus* Aust. (*S. californicus* Aust.) (13). I shall, in the near future, publish my results on this phase of the life history of *Thallocarpus*.

Material for this study was collected during the months of March, April, and May of the years 1914 and 1915. Weak

Flemming's solution gave perhaps the most successful fixation though there was no marked difference in the action of the killing solutions used. The gelatinous material of the older sporophytes interfered greatly with the penetration of the reagents, though an air pump was used to hasten the penetration of the liquids.

The thallus of *Thallocarpus* varies greatly in size. Mature sporophytes may be found in thalli with a diameter of but two millimeters, while in late spring sterile thalli may be found which have a diameter as great as fifteen millimeters. The male plants rarely exceed three or four millimeters in diameter, the average diameter being less than three millimeters.

When very young the thallus is distinctly bilobed, having a single distinct growing area. The mature male plants are usually bilobed only. The female thalli usually become symmetrically four-lobed but later the lobing becomes less regular and in the larger thalli there is often a suggestion of palmate lobing with the lobes often crowded and overlapping.

The thallus is very spongy in texture, resembling in this respect the spongy Riccias. Many irregular openings are visible in the upper surface. As is the case with the spongy Riccias the thallus is pale green in color. Superficially it resembles *Riccia crystallina* L.

Cross sections of the thallus show it to be made up, in the upper part of the thallus, of irregular plates of cells, mostly a single layer in thickness. At the upper surface these plates are broadened greatly to form the upper "epidermis" (FIG. 1). The tissue at the base of the thallus is compact with but few intercellular spaces.

The archegonia begin development at the surface of the thallus just back of the growing point. The mother cell of the archegonium elongates and divides transversely, the upper cell being the smaller (FIG. 2). The lower cell divides again by a transverse wall (FIG. 3) which according to Campbell (6) also occurs in the development of the archegonium of *Sphaerocarpos* while in *Riccia* this cell remains undivided. The divisions of the upper cell seem to be the same as in *Riccia*. The general structure of the mature archegonium does not present anything new. The neck canal cells seem to number four or five (FIGS. 4, 5).

As the archegonia develop, plates of cells are formed about them in such a manner as to entirely submerge them at maturity.

The antheridia arise back of the growing point of the male thallus in much the same position as the archegonium appears in the female plant. I have not followed the development of the antheridium in detail but there seems to be no noteworthy difference between them and those of *Riccia*. From Figs. 6 and 7 it will be seen that the early stages of development conform entirely with those of *Riccia*, according to the accounts of Garber, Campbell, and Lewis.

The fertilized egg divides by a wall transverse to the long axis of the archegonium (Fig. 8) as is the case with *Riccia* and the other Marchantiales. The subsequent divisions seem also to be the same as in *Riccia*, forming finally a sphere eight to ten cells across at the longest diameter. Divisions cease in the mass of sporophytic cells when the sporogonium is about half grown (Fig. 10). At this period the cells are all alike, no difference being observable between the cells that are later to form the wall and those that are to form the spore mother cells.

Frequently, however, a number of sporophytic cells adjoining the neck canal, fix and stain differently from the rest of the cells of the sporophyte. They are usually smaller cells with denser protoplasmic content and with nuclei which are smaller and which take the stain more readily than those of the other cells of the sporophyte. From Figs. 9, 10, 11, and 12 it will be seen that they occur in sporophytes of all ages, except possibly those fully mature. Miss Black (5) has observed bacteria accumulated at the base of the neck canal in *Riccia Frostii* Aust., causing injury to the sporophytic cells of this region. It is possible that the above mentioned cells of the sporophyte of *Thallocarpus* may have been injured by secretions of bacterial origin though I have never observed bacteria-like structures in this region.

The single layer of cells of the venter divides early to form two layers (Fig. 9). These cells enlarge with the division and enlargement of the cells of the sporophyte but do not themselves undergo further division. Their dimensions at the maturity of the sporophyte are at least three times as great as at first (Figs. 12, 13). The outer layer of venter cells is seen early to be abundantly supplied with chloroplasts while the inner layer lacks them (FIGS. 11, 12). As the spores mature the inner of the two layers of venter cells is crushed and absorbed while the outer layer remains intact, forming a persistent layer about the mass of spores (FIG. 14).

The cells of the sporophyte are probably more than half grown before any difference is perceptible between the cells of the amphithecium and the sporogenous cells (FIG. 9). This difference is first seen in a decrease of the protoplasmic content of the peripheral cells, and a possible increase in the density of the protoplasm of the sporogenous cells (FIG. 10). Later, as the sporogenous cells continue to enlarge, a difference in the size of the cells is apparent. At the time of the rounding up of the spore mother cells before division, the cells of the peripheral layer have a very scanty protoplasmic content and small, degenerate nuclei. The cells are however plump and distended with cell sap and do not show signs of collapse till much later (FIG. 12). Their collapse and disintegration at a later stage greatly enlarges the cavity in which the spores lie (FIG. 13).

Beer (4) has observed similar, large, vacuolate cells making up the amphithecium of *Riccia glauca* L. Garber (7), Campbell (6), and Lewis (9) have, however, described the amphithecium of *Riccia* as made up of flat cells which have dense contents.

The rounding up of the spore mother cells previous to the reduction divisions is accompanied by a swelling and gelatinization of the cell walls (FIG. 12). The gelatinous material accumulates in the spaces between the now rounded spore mother cells (FIG. 13) where it interferes greatly with the penetration of the killing solutions. In fixed material it stains deeply with the violet stain. Garber and Lewis have both observed such gelatinous accumulations in *Riccia* and are of the opinion that it is food material, derived, in part at least, from the surrounding cells, which are believed to be abundantly supplied with food material. In *Thallocarpus* this is not the case. No excess of food is to be identified in the surrounding cells nor is there any marked change in these cells upon the appearance of the gelatinous material. The gelatinization of the walls of the spore mother cells together with the disintegration of the wall layer of cells seems sufficient to account for the amount of gelatin formed.

The gelatinous material persists for some time, disappearing only as the thick common wall is formed around the spore tetrad (FIG. 14). The sporogenous cells all round up to form spore mother cells and all of the spore mother cells undergo division and all of the resulting cells form spores. None become sterile nutritive cells nor elater-like cells.

After the division of the spore mother cell the resulting cells become separated by a thin wall but remain closely attached and finally become surrounded by a thick, papillate common wall (FIGS. 14, 15). These spore walls remain thin and undeveloped until the thick retaining wall of the spore ball is completely formed (FIG. 14). The outer face of the tetrahedral spore is slightly roughened with projections which in cross section appear crenulate (FIG. 16). While thickened to a marked degree the wall of this outer face is not more than half as thick as the retaining wall of the spores of the tetrad. The inner faces of the spore are thickened only slightly.

It will be seen from the above that the structure and the development of the gametophyte and the sporophyte of *Thallocarpus* is practically identical with that of *Riccia.* The adhesion of the spores of the tetrad in a spore ball and the lack of peg-like thickenings in the rhizoids of the former are the only characters upon which a separation of the two genera could be based.

The morphology of the plant is nevertheless that of a *Riccia* rather than of a *Sphaerocarpos.* The adhesion of the spores is certainly very scanty evidence upon which to base relationship to the latter genus, for not all of the *Sphaerocarpos* species have spores remaining attached at the time of their shedding. The spores of *S. cristatus* M. A. Howe separate long before maturity and those of *S. Donellii* Aust. separate as they come to maturity (**8**).

The occurrence of peg-like rhizoid thickenings throughout the Marchantiales and their lack in the Jungermanniales may be a character of greater phylogenetic significance. While it is probable that this character should receive more consideration than the spore characters, nevertheless, in view of the essential identity of the structure of the gametophyte of *Thallocarpus* with that of *Riccia*, it would seem extreme to remove the genus *Thallocarpus* from the Marchantiales on the grounds of this character alone.

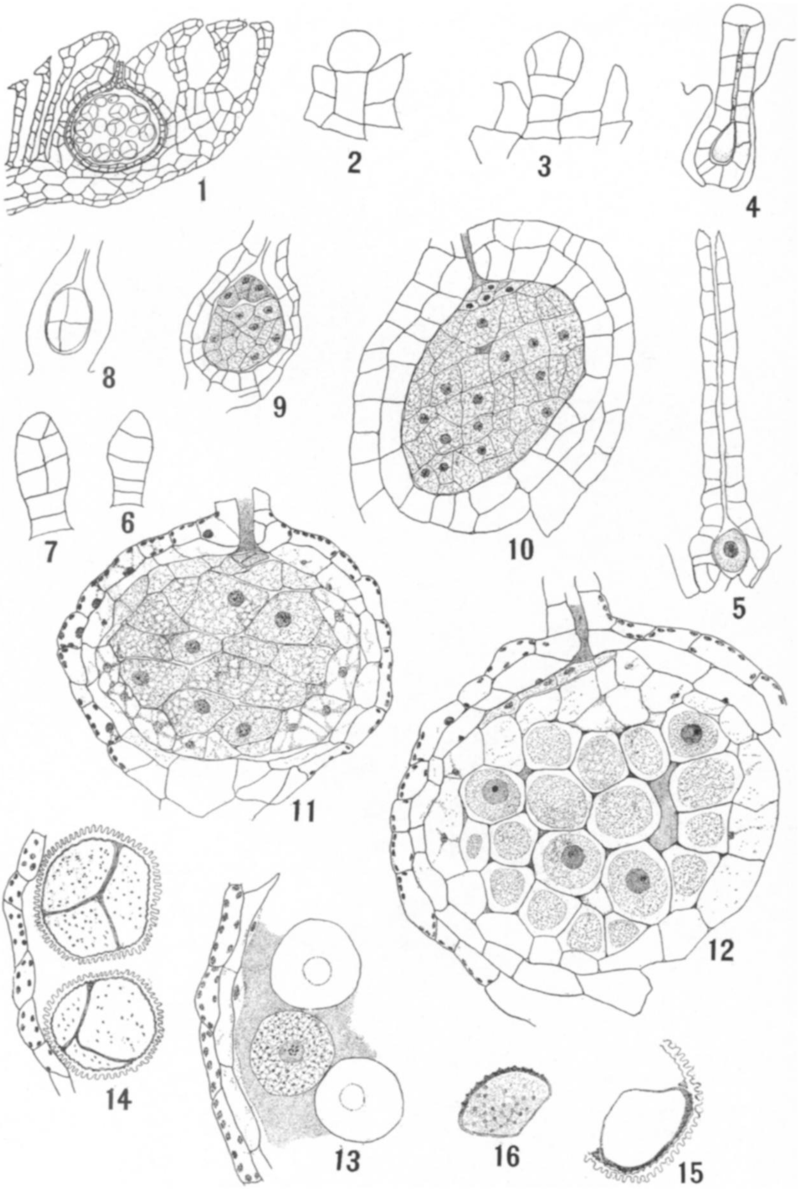
The monoecious plants which Stephani believed he had found may possibly be explained on the ground of the small size of the male plants and the crowded growth of the thalli, which become attached in masses by the rhizoids. The male plants cease growing early and are often entirely overgrown by the female plants. In dry material it would be difficult to separate the plants or even to identify any organic separation. This is often difficult in living material collected early in the season. Two cases of what seemed at first to be monoecious plants in paraffin sections turned out to be distinct plants, the male plant being entirely covered by the female plant. There seems little doubt that the Texas *Thallocarpus*, at least, is dioecious.

SUMMARY

1. *Thallocarpus*, as it occurs in the vicinity of Austin, Texas, seems to be strictly dioecious.
2. The spores of the tetrad adhere after shedding and give upon germination two male and two female plants.
3. The structure of the thallus and the sporophyte is identical with that of the Riccias with the exception of the adhering spore tetrads and the pegless rhizoids.
4. The above mentioned structural differences seem insufficient to exclude *Thallocarpus* from the Marchantiales.

I am indebted to Mr. F. C. Werkenthin, of State College, New Mexico, for valuable aid in preparing sections for this study.

UNIVERSITY OF TEXAS,
AUSTIN, TEXAS



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Explanation of plate 4

The magnification of the figures is about 250 diameters, with the exception of FIG. 1, which is magnified about 30 diameters.

FIG. 1. A portion of a section of a thallus, showing a sporophyte, nearly mature.

FIGS. 2, 3. Early stages in the development of the archegonium.

FIG. 4. Archegonium, not quite mature, becoming submerged by outgrowths of the thallus.

FIG. 5. Archegonium after fertilization of the egg.

FIGS. 6, 7. Early stages in the development of the antheridium.

FIG. 8. A four-celled embryo sporophyte.

FIG. 9. A later stage in the development of the embryo. Venter wall two cell layers in thickness. A group of cells at the apex of the sporophyte separated from the main mass.

FIG. 10. Embryo about half grown. No distinction visible between the peripheral cells and the inner cells of the sporophyte.

FIG. 11. Peripheral cells of sporophyte now easily identified by their scanty protoplasmic content.

FIG. 12. Gelatinization of the cell walls and the rounding up of the spore mother cells. Cells of the amphithecium still plump and intact.

FIG. 13. Spore mother cells fully rounded up and surrounded by the homogeneous gelatinous material. Peripheral layer of cells disintegrated. Venter cells still intact.

FIG. 14. Spores approaching maturity. The papillate retaining wall of the spore ball nearly mature. The spore walls still thin.

FIG. 15. One spore and part of the common retaining wall.

FIG. 16. Section of nearly mature spore, pulled away from spore ball by sectioning knife.